GENETICS VERSUS PALEONTOLOGY

DR. WILLIAM K. GREGORY

AMERICAN MUSEUM OF NATURAL HISTORY

ALTHOUGH the title of this article has a somewhat controversial sound, its purpose is merely to discuss, in a perfectly frank and appreciative way, certain passages in the
recent works of two eminent geneticists, Professor William Bateson and Professor T. H. Morgan.

"Naturally," says Professor Bateson,[1] in describing a
certain theoretical *impasse* as regards the method of evolution, "we turn aside from generalities. It is no time to
discuss the origin of the Mollusca or of Dicotyledons
while we are not even sure how it came to pass that
Primula obconica has in twenty-five years produced its
abundant new forms almost under our eyes."

Taken in connection with other passages, this seems to
imply the belief that the present is no time to investigate
phylogenetic problems or to formulate any generalities
concerning the origin of systematic groups of organisms.
Until the facts of heredity are explained we should turn
aside from most of the major problems that engaged the
attention of the great comparative anatomists and paleontologists of the nineteenth century. The origin of
paired limbs, the origin of the vertebrates, the mutual relations of the great phyla of invertebrates, and similar
phylogenetic problems in botany, all these and hundreds
more of the same category having been laid aside by the
majority of zoologists, are dead or moribund subjects
which a student of genetics had better leave in decent obscurity. If Professor Bateson had said "I turn aside
from generalities. I have no time to discuss the origin of
the Mollusca or of Dicotyledons. I used to be interested
in such things, but now I would much rather study the
mutations of *Primula obconica*," nobody could reasonably
object; but when he says "*we* turn aside from generalities.
It is no time [for any one] to discuss the origin of the

[1] *Science*, N. S., Vol. 40, 1914, p. 294.

Mollusca . . .,'' etc., he is apparently mistaking a part for the whole, and also confusing two fairly distinct lines of investigation, genetics and phylogeny.

As long as museums and universities send out expeditions to bring to light new forms of living and extinct animals and new data illustrating the interrelations of organisms and their environments, as long as anatomists desire a broad comparative basis for human anatomy, as long as even a few students feel a strong curiosity to learn about the course of evolution and the relationships of animals, the old problems of taxonomy, phylogeny and evolution will gradually reassert themselves even in competition with brilliant and highly fruitful laboratory studies in cytology, genetics and physiological chemistry. Very likely the fortunate few who gain some first-hand knowledge in all these fields will realize that such problems as the origin of the Mollusca or the origin of the Dicotyledons have as much vitality as the problem of the origin of the earth or the problem of the phyletic relationship of man with the lower animals.

The student of the evolution of the vertebrates may well reserve judgment as to theories of evolution, and he must even confess his inability to trace a detailed phylogenetic succession except for short intervals; yet he is well assured, from long experience with the paleontological record and with the comparative anatomy of recent animals, that he can trace in a general way the history of many groups and of many structures, and he should know very definitely where the evidence is fairly complete and where it is weak and lacking. In view of the wealth and detailed character of the evidence (which is hardly known except to a limited number of specialists) no competent authority would doubt, for example, that all the races of modern Equidæ, walking on the tips of their one-toed feet, have been derived from three-toed *Hipparion*-like forms, or that these in turn lead back to *Eohippus*-like forms of the Eocene, with four digits on each forefoot and three on each hind foot; or that during the Tertiary Period the molar teeth of horses (in the broadest sense) changed

from low-crowned teeth of simple pattern into long-crowned teeth of a complex pattern. And even in the practical absence of paleontological evidence it is sufficiently established that the Cetacea, which are now of pelagic habit and fish-like habitus, represent transformed terrestrial or littoral quadrupeds, which at a remote epoch were placental mammals of some sort. Nor can it be justly doubted that birds are ''glorified reptiles,'' that bats are volant derivatives of arboreal mammals, that teleosts have been derived from ganoids. Detailed knowledge of the evidence in hundreds of such cases leads the paleontologist to say with considerable confidence: ''this later type of animal has probably been derived from that earlier type; this structure has undergone such and such changes during certain geological periods.''

Professor Bateson is equally cold towards outworn notions about adaptation. ''Naturalists may still be found,'' he says,[2] ''expounding teleological systems which would have delighted Dr. Pangloss himself, but at the present time few are misled. The student of genetics knows that the time for the development of theory is not yet. He would rather stick to the seed-pan and the incubator.''

Two very distinct ideas seem to be implied in this passage and the context, first the rejection of the supposed principle of progressive adaptation in evolution, and secondly the idea that conclusions regarding evolution should be limited to those in which control experiments can be made.

As to the principle of progressive adaptation, it is an indisputable fact that existing animals possess structures which are highly efficient in the performance of certain functions, *e. g.*, the locomotive apparatus of the horse, effective for progression over hard ground; its masticatory apparatus, effective in the trituration of siliceous vegetation. Paleontologists, after studying the phylogenetic history of such structures, must infer that progressive advance of structure has been influenced to a

[2] *Ibid.*, p. 293.

greater or lesser degree by environmental conditions. It is certain that changes in the conditions of life are not the sole causes of modification, it is highly probable that the chromosomes are insensitive to most somatic reactions to the environment; yet how can the student of the Cetacea, who sees how thoroughly the ancestral quadrupedal heritage has been overlaid by the fish-like habitus, doubt that in the end, and perhaps in some very indirect way, the pelagic environment has conditioned the line of evolution of the cetacean chromosomes, as it plainly has conditioned the evolution of cetacean cytoplasm. And when similar adaptations are produced among widely separate stocks, it can scarcely be doubted that the similar results are due to the similarity of the external conditions as well as to the fundamental similarities of all cytoplasm and of all chromatin. Hence, without any commitment as to the mode of evolution, paleontologists adopt the principle of progressive and retrogressive adaptation to environmental conditions as sufficiently demonstrated. And most paleontologists would probably recognize that the foot, for example, is just as much a part of the environment of the femur as is the medium upon which the foot rests, in other words that evolution of a given structure is conditioned by its internal environment as much as by external environment.

Yet such is the skepticism which sometimes results from modern studies in genetics that I have known graduate students who seriously doubted the reality and value of the principle of progressive and retrogressive adaptation, on the ground that, as natural selection and the inheritance of "acquired" characters had both been disproved, there was no conceivable means whereby adaptation could be brought about! But if these skeptics would study for example the evolution of Triassic ganoids into Cretaceous and modern teleosts, if they would consider in detail the structural improvements in the locomotive apparatus of teleosts, which involve the transformation of scales into dermal rays, or of a heterocercal tail into a homocercal tail, or if they would examine the evidence

bearing upon the evolution of the paired limbs or upon the evolution of the vertebrate skull, or of the carnassial teeth of Carnivora, they would, I believe, be forced to accept the principle of the progressive efficiency of structures for special functions as at least a fruitful working hypothesis.

A distrust of the word "adaptation," which has been in the bad company of the Lamarckian theory, is apparently revealed in Professor T. H. Morgan's "A Critique of the Theory of Evolution" (1916). The author, however, apparently favors the idea of natural selection operating upon "advantageous" or "beneficial mutations" and eliminating the "injurious effects" of other mutations. Of course if "adaptation" really implied an acceptance of the Lamarckian theory it would be better to use some such phrase as "progressive functional adjustment," but the important point to bear in mind is that nature has produced myriads of structures which have a very definite functional adjustment with other structures, in other parts of the body, or with parts of other bodies, or with parts of the environment. And it is perfectly plain from the evidence of comparative anatomy and paleontology that functionally correlated parts have often evolved together, and with definite reference to each other, let the explanation of that fact be what it may. Professor Morgan himself has fully recognized this fact in his address[3] entitled "Chance or Purpose in the Origin and Evolution of Adaptation."

The second idea which seems to be implied by Professor Bateson, and which I have heard certain university students express, is that phylogenetic "speculations" are unverifiable, because "control experiments" are not possible. By similar reasoning geological theories concerning the history of the earth, archeological theories concerning the history of peoples, and all historical studies based upon internal or circumstantial evidence are equally untrustworthy. The answer to such a theoretical objection, if it were definitely made, would be that comparative

3 *Science*, Vol. 31, 1910, pp. 201–210.

anatomy, geology, phylogeny, etc., are practical arts which have to be learned by experience. Phylogenists must constantly distinguish between primitive and specialized characters, and if their experience, caution and judgment be adequate they may be as successful as physicians are in diagnosis. Of course physicians make mistakes and so do phylogenists, but in the long run both succeed in sifting the false from the true, even without the aid of direct experimentation. Nature herself often provides control experiments, as when she forces animals of widely different stocks into similar life habits, or when she takes a primitive type of skull and dentition and molds them into a wide variety of adaptive types, meanwhile preserving the original pattern as a "control," either in the form of a "living fossil," persisting in a primitive environment, or in the form of a real fossil found in Tertiary strata.

Professor Morgan makes a serious and important criticism of the comparative anatomical and paleontological doctrine that structures have been derived by progressive continuous stages. He is evidently inclined to think that structures have rather been derived through discontinuous mutational stages. It would be easy, he shows, to arrange a graded series of fruit flies belonging to distinct mutations, having at the one extreme perfectly formed wings and at the other extreme no wings at all. But this series by no means represents the historical order of appearance of these mutants, which are not genetically derived one from the other, but have arisen independently. Again (p. 13)

. . . it is easily possible beginning with the darkest eye color, sepia, which is deep brown, to pick out a perfectly graded series [of races] ending with pure white eyes. But such a serial arrangement would give a totally false idea of the way the different types have arisen; and any conclusion based on the existence of such a series might very well be entirely erroneous, for the fact that such a series exists bears no relation to the order in which its members have appeared.

"Suppose," he continues, "that evolution 'in the open' had taken place in the same way, by means of *discontinuous* variation. What value then would the evidence [for

evolution] from comparative anatomy have in so far as
it is based on a continuous series of variants of any
organ?''

We may readily admit that *if* evolution in the open has
taken place through discontinuous variation, the supposed
evidence for evolution based on continuous series of va-
riants is valueless. But neither Professor Morgan nor
the present writer try to persuade students of the truth
of evolution upon the ground that supposedly continuous
series have been traced purporting to illustrate the evo-
lution of *single* structures. As he well intimates, the
strongest evidence for evolution is the fact that all the
widely diverse members of each group exhibit a common
heritage or ground-plan of homologous structures. When
that common ground-plan is recognized and when the
probable habits of the ancestral form are clearly per-
ceived a long step has been taken toward deciphering the
evolutionary history of the group; and it will often be
easy to decide what characters and habits have been lost
and what new ones have been acquired.

Whether we think evolution has taken place by means
of discontinuous variation or through regular progressive
and continuous series one of the chief aims of zoologists
is, or should be, to discover the facts concerning the
phyletic interrelationships of groups and the evolution of
their habits and structure. And often the chief earlier
and later stages might be recognized in spite of ''discon-
tinuous variation.'' For example, if one knew nothing
about the history of the mutant races of *Drosophila* it
would seem a safe inference that the apterous form had
been derived eventually from a winged type, because a
comprehensive study of Diptera in general would indicate
that wingless flies were degenerate and not primitive in
that respect. Similarly if the systematic relationships
and probable derivation of *Drosophila* were given due
consideration the races with imperfect eyes and those with
duplicated parts would naturally be regarded as degraded
or aberrant, rather than original or primary types; and
if many intermediate stages between winged and wingless

forms were found living at the same time in a restricted area one might perhaps have suspected that these contemporaneous intermediate forms were parallel offshoots of a normal parent stock rather than linear descendants one of another.

It may well be true that, until it can be shown that evolution "in the open" is continuous and not discontinuous, all "laws" and "principles" which merely assume such continuity are open to question. But there is considerable evidence for the conclusion that many races of mammals have evolved either quite continuously or by small *successive* gradations. It is true that in some cases apparently new and distinct forms also appear in successive horizons, but these new forms may be immigrants from other distribution centers[4]—the little-modified descendants of indigenous races being often found side by side with their more progressive immigrant relatives.

The great collections of American Eocene and later mammals which have been brought together by the systematic explorations of the American Museum of Natural History are all exactly recorded as to level, so that except in a few instances there can be no doubt whatever as to the chronological sequence of the specimens. These collections, numbering many thousands of specimens, are being minutely studied by several investigators, who are not trying to prove any theory of evolution, but are recording and identifying specimens and analyzing their observations, with such accuracy and judgment as they may have gained from twenty years of experience in this work.

The results of these studies, as bearing on the question of continuity *vs.* discontinuity in evolution, are too extensive and complex to be summarized here, but a few examples may serve to illustrate the kind of evidence available and the conclusions which have been drawn in typical instances.

Very often as we pass from lower to higher strata of

4 Matthew, W. D., "The Continuity of Development," *The Popular Science Monthly,* Nov., 1910, pp. 473–478.

a given formation the successive species show a regular increase in size and a progressive molarization of the pattern of one or more of the premolar teeth. A typical case of this kind is recorded by Matthew[5] in the genus *Cynodontomys,* a small insectivorous mammal of the Lower Eocene which is represented by three successive species which do not overlap in time, but are separated by small progressive differences in the premolars and molars. Each species is represented by series of from ten to twenty specimens, from successive horizons of the Bighorn and Wind River Basins in Wyoming. Another instance of practically continuous evolution is furnished by the Middle Eocene titanothere *Palæosyops.* Professor Osborn and the present writer have observed that in this genus the species named *paludosus, major, leidyi* and *robustus* form a regular and nearly continuous series extending from the lower to the higher levels of the Bridger Basin, in which the lower and upper premolars gradually evolve toward the molar pattern. A fifth species, *P. copei,* from the uppermost fossiliferous levels of the Bridger Basin is considerably more advanced than any of its predecessors, and is connected with them by intermediate specimens from the nearby Washakie Basin of the same age.

In other cases the material indicates that while some phyla evolve at a nearly uniform rate others lag behind at varying rates, the extreme cases furnishing the relicts or "living fossils" which give so many useful hints as to the primitive characters of a race.

Such an instance is furnished by the history of the Eocene primates *Pelycodus* and *Notharctus* (Table I). The oldest species, *Pelycodus ralstoni,* is of small size and very primitive character. The latest species, *Notharctus crassus,* is about twice as large and of very advanced character. Many intermediate stages are known. Of these *P. relictus* is an extremely conservative form which has acquired only a few of the progressive characters seen in its contemporaries.

[5] *Bull. Amer. Mus. Nat. Hist.,* Vol. XXXIV, 19, p. 470.

TABLE I

PROGRESSIVE INCREASE IN THE LENGTH OF THE LOWER MOLARS (m_{1-3}) IN LOWER AND MIDDLE EOCENE LEMUROIDS OF THE FAMILY ADAPIDÆ (SUBFAMILY NOTHARCTINÆ)

Data for Lower Eocene species compiled from Matthew (*Bull. Amer. Mus. Nat. Hist.*, Vol. XXXIV, 1915, p. 436. Data for Middle Eocene species by Granger and Gregory.

	HORIZONS		
MIDDLE EOCENE	UPPER BRIDGER Bridger Basin, Wyo.	pm^4 with two large external cusps, m^{1-3} with large mesostyle, molars quadritubercular.	*N. crassus* 20.7–23.5 mm.
	LOWER BRIDGER Bridger Basin, Wyo.	*P. re-* *N. for-* *an-* *ty-* *tene-* *ros-* *pug-* *lictus* *mosus* *ceps* *affinis* *rannus* *brosus* *tratus* *nax* 15 16.6 17.5 18 18 est. 18.6 19 20.7	
LOWER EOCENE	LOST CABIN Wind River Basin, Wyo.	*Notharctus nunienus* 15.5	*N. venticolus* 18–19.2
	ALMAGRE * (San Juan Basin, N. M.) LYSITE Bighorn Basin, Wyo.	*Pelycodus frugivorus* 14–16 *P. jarovii*	*P. tutus* 19
	UPPER GRAY BULL Bighorn Basin, Wyo. LOWER	*P. frugivorus* *P. jarovii·* 16–18 *P. trigonodus* *P. jarovii* (rare) 15 *P. ralstoni*	
	SAND COULÉE Clark's Fork Basin, Wyo.	*Pelycodus ralstoni* 11–14 mm.	pm^4 with 1 external cusp, m^{1-3} without mesostyle, molars tritubercular.

* The upper levels of the Almagre of New Mexico are perhaps equivalent to the Lysite. Granger, *Bull. Amer. Mus. Nat. Hist.*, Vol. XXXIII, 1914, p. 207.

In certain cases the paleontological evidence is indecisive, as between the hypothesis of successive mutation *in loco* and the hypothesis of continuous evolution in an unknown center of evolution followed by discontinuous immigration of later stages into the region under observation. Such a case is described by Matthew[6] as follows:

[6] *Bull. Amer. Mus. Nat. Hist.*, Vol. XXXIV, 1915, p. 316.

Osborn in 1902 pointed out the evolutionary progress observable in the species of *Hyopsodus* from successive stages of the Lower and Middle Eocene; this is in general confirmed and extended by the far larger collections [comprising more than a thousand specimens] now available and the somewhat wider geologic range of the genus; but it is evident that not one but three or four phyla are present in each horizon; the relations of the Lower Eocene species to those of the Middle Eocene are not wholly clear, and the geological overlap of stages of each structural phylum suggests rather progressive displacement of older by newer stages coming in from some other region, than gradual evolution *in loco*. It might equally well be interpreted as the displacement of older by newer " mutants," in the DeVriesian sense of the term.

However this may be, the Lower Eocene species are distinguished from those of the Middle Eocene by the less molariform premolars, and this is most noticeable in *H. simplex* from the lowest horizon, while the Lost Cabin species [from the upper part of the Lower Eocene] approach nearest to those of the Bridger [Middle Eocene].

Examples of this kind might be multiplied, tending to show that the evolution of Tertiary mammals has often been more or less continuous, or by small successive changes, at least during the relatively brief geological periods that are represented by a large series of specimens from closely sequent levels of an uninterrupted stratigraphic series. And although mutations may well be a paleontological reality, there is little danger that vertebrate paleontologists are likely to draw false inferences regarding the history of structures and of races through mistaking independent contemporaneous mutants for successive stages, for the simple reason that their observations are based on long series of specimens which are arranged in their true chronological sequence, from ascending geological horizons covering the whole Tertiary Period.

In this connection I submit an accurate diagram (Fig. 1) by Mr. Granger, which is fairly representative of the kind of evolution demonstrated among many, but not all, known races of mammals during the Tertiary and Quaternary Periods, a period of time conservatively estimated at 4,000,000 years.

The character of the evidence tending to show that the paleontologist is dealing with truly successive stages and
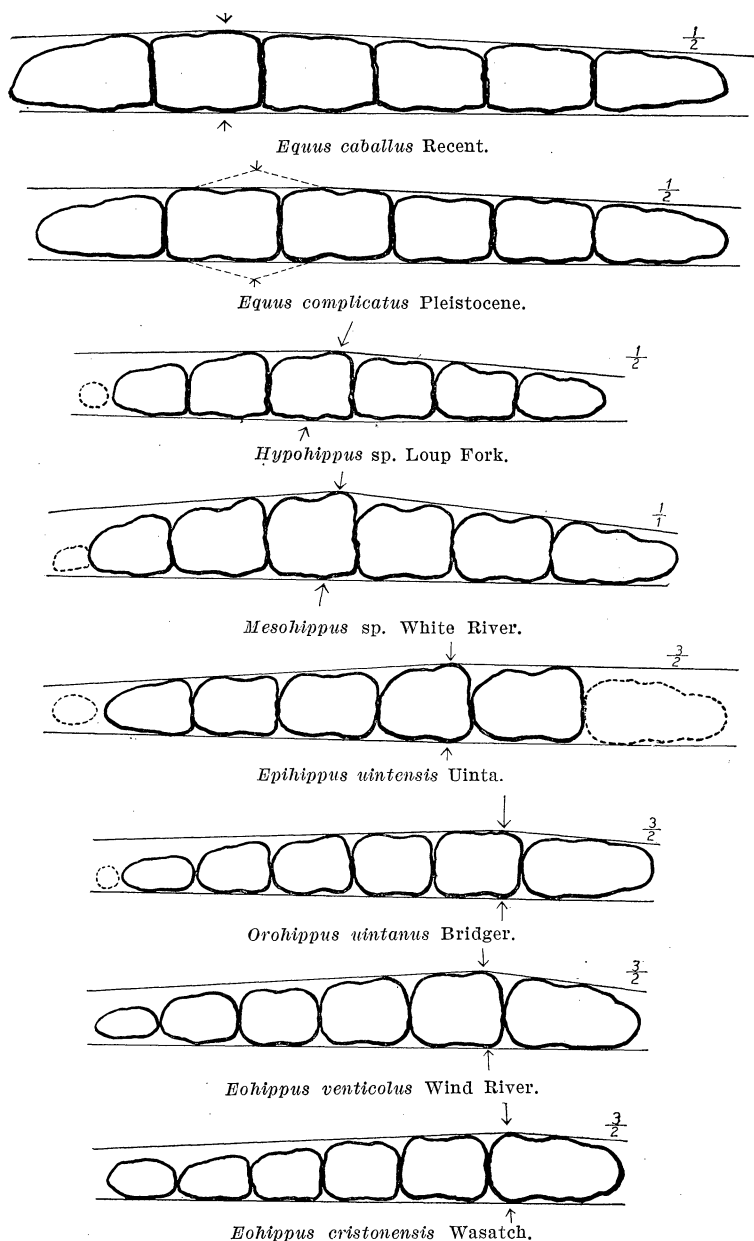
FIG. 1. Accurate outlines of lower cheek teeth of Equidæ. Arrows indicate point of greatest transverse diameter in each series, ranging from the third molar in the Wasatch species to the third premolar in the modern Equidæ. After W. Granger (*Bull. Amer. Mus. Nat. Hist.,* Vol. XXIV, Art. XV, pp. 221–264, 1908.)

not with an arbitrarily selected series of mutants is further illustrated in the following note by Dr. Matthew.

Of the hundreds of specimens examined no horse from the Lower Eocene has ever been found which had *any* fully molariform premolars. No horse out of the Middle Eocene has either more or less than *one* molariform premolar in the lower jaw, on each side. Out of the Upper Eocene all horses have *two* molariform premolars. In the Oligocene all have *three*. All Oligocene and older horses have brachyodont molars without cement. All Miocene horses are progressively hypsodont with a progressive increase in the amount of cement. The milk teeth of Miocene horses have almost no cement. Those of all Pliocene and later horses are heavily cemented. At each successive stage of evolution the cement appears at an earlier stage in the ontogeny of the tooth. These are simply a few out of many progressive changes in the teeth, and they are accompanied by equally clear progressive changes in the skull and skeleton. Every one of these progressive stages is as exactly limited in time as the ones cited.

Geneticists who are examining the nature of the paleontological evidence regarding modes of evolution would do well to realize that only a small part of the available material bearing on the subject is either exhibited or published. The scientific staff of the American Museum of Natural History would be very glad to exhibit to their colleagues the great wealth of accurate data, concerning the chronological sequence of specimens, which has been gathered during twenty years of close exploration; they would also be pleased to place before them any of the extensive series of specimens, sometimes amounting to several thousands of individuals, which appear to throw light upon the problem of continuity *vs.* discontinuity.

In conclusion, paleontologists can show that evolutionary changes have involved *progressive and measurable emphases or suppressions of earlier structures or of earlier proportions* (allometric evolution, Osborn); and when the progressive emphases are manifested as focal outgrowths they seem like "new" structures (rectigradations, Osborn). Paleontologists, however, are not in a position to say which characters would be transmitted according to the Mendelian ratio, nor can they prove what were the cytological causes of the evolutionary changes

which they record or infer. In that direction lies opportunity for consultation with the men who study enzymes, chromosomes, heredity and variation.

The Batesonian hypothesis that both the progressive differential emphases or suppressions of organs, and the focal outgrowth of new structures, have been due to a secular, differential stopping down of inhibitory factors inherent in the germ-cells seems to the present writer quite consistent with the observed facts of evolutionary change; but apparently no observations that the paleontologist can make could furnish any critical tests of this hypothesis; it therefore has for him a stimulative philosophical value, but hardly constitutes a working hypothesis for the discovery of new facts and principles in his limited field.

The nature of later events being determined in part by the nature of their precedent events, no matter how many causal series may be interwoven in the final outcome, it follows that paleontologists, like other historians, contribute to a partial understanding of existing conditions merely by arranging past events in their true chronological sequence. The characteristics of existing Cetacea are determined in part by the germinal and somatic characteristics of their remote quadrupedal ancestors, as well as by the conditions of the pelagic life into which they somehow drifted; so too the characteristics of man, as a bipedal, bimanous, anthropoid Primate are determined in part, as I believe, by the fact that the remote ancestors of the man-greatape stock were arboreal, quadrumanous, lemuroid Primates of the Lower Eocene.

For such reasons, I must continue to hold that "progressive adaptation" when cleared of all implications as to the mode of evolution, stands for a historical and verifiable process; that the time for developing phylogenetic conclusions and for revising comparative anatomy and classification is always *now*, as fast as the evidence can be gathered and analyzed.